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Developmental and Environmental Effects on Assimilate Partitioning in Canada Thistle (*Cirsium arvense*)[1]

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Abstract. **Under field conditions, more photoassimilate moved to roots of Canada thistle at the bolt than at the bud, flower, or postflower stages. Similarly, greater photoassimilate accumulated in roots of Canada thistle in the greenhouse at the rosette and bolt than at the flower bud stage. Growth chamber experiments indicated that environmental conditions typical of fall, and possibly early spring, favored photoassimilate movement to the root and superseded growth stage control of assimilate partitioning. Allocation of assimilate within the root was strongly influenced by growth stage, with most assimilate being utilized for growth at the rosette stage and for fructan reserves in bolt and flower bud stages. Nomenclature: Canada thistle, *Cirsium arvense* (L.) Scop. #[3] CIRAR.**

Additional index words. **Phloem transport, carbohydrate reserves, fructan.**

INTRODUCTION

Canada thistle is a noxious weed in the Northern United States and southern Canada (20). It can spread by roots at a rate of 1 to 2 m per year and secondary shoots develop adventitiously from the root system (1). Secondary shoots or germinated seedlings emerge from soil under spring conditions in Maryland, appear as a rosette for 2 to 4 wk, undergo shoot elongation (bolt), and form flower buds approximately 10 wk after emergence. Secondary shoots emerge in late summer and fall and develop into rosettes and bolted plants. Thus, Canada thistle populations may consist of several growth stages in spring or fall. Canada thistle's vigor has been related to carbohydrate reserves and susceptibility to herbicides may be associated with its carbon economy, including partitioning in the phloem (8).

Carbohydrates accumulate in the perennating root of Canada thistle (2). Root carbohydrate reserves decline from May through early June or July, followed by an increase through September (2, 9, 26, 29). Carbohydrate decline was hypothesized to be associated with root carbohydrates supplementing photosynthate for shoot growth and respiration during onset of growth in the spring (2). The nadir of root carbohydrate levels varied with year, occurring both before and after flower bud development (9). Flowering and accumulation of root reserves were synchronous (26). Collectively, these studies demonstrated that root carbohydrate depletion occurred at several growth stages in the spring and early summer. However, root carbohydrate replenishment occurred only in late summer and fall, suggesting that environment, rather than growth stage, controls replenishment.

Environmental conditions influence Canada thistle root carbohydrate accumulation at flower bud development (9) and flowering (22). Root-to-shoot ratio was greater when Canada thistle was grown at 16 than 21 C (1.6 and 0.5, respectively) (11). A greater root-to-shoot ratio occurred under a 15/5 C (day/night) than a 25/15 C or a 30/22 C temperature regime (10). It was hypothesized that assimilate transport to roots occurred readily when root respiration was low. Belowground nonstructural carbohydrate levels were greater in a Canada thistle ecotype grown at 10 than 27 C (16).

Temperature influenced assimilate transport into roots and total carbohydrate accumulation. Translocation of ^{14}C-assimilate from leaves of Canada thistle was greater under lower shoot (15/5 C, day/night) and root (10 C) temperatures than higher temperatures (18). Photoassimilates in quackgrass [*Elytrigia repens* (L.) Nevski] translocated more readily to rhizomes at soil temperatures of 12 than 18 C (15).

Developmental growth stage of Canada thistle may also affect photoassimilate export and partitioning. Environment was responsible for short-term changes in Canada thistle root carbohydrates but physiological changes associated with flowering accounted for late-summer accumulation of root reserves (4). During the 12- to 20-d period following shoot emergence, increasingly more ^{14}C-assimilate translocated to roots (17). However, more ^{14}C was retained in the shoot by 30 d, presumably because the shoot became a more competitive sink.

Effect of environment and developmental growth stage on carbon allocation to specific carbohydrates within Canada thistle is not well known. Inulin and sucrose were the principle carbohydrates in Canada thistle roots, together with smaller amounts of maltose, fructose, and glucose (23). Starch was not found in Canada thistle roots (22). Distribution of assimilate among carbohydrate components in plants grown under various environmental conditions is of particular interest since Canada thistle is a fructan-storing plant (23). Fructan metabolism has been implicated in physiological functions such as cold hardiness and phloem transport (21). A clearer understanding of carbon distribution among carbohydrate pools in Canada thistle may provide insight as to the physiological basis for its ecological niche.

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[3]Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Revised 1989. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.

The present research examines effects of environment and stage of development on partitioning and fate of photoassimilates in Canada thistle. Objectives were to determine the influence of growth stage and environment on photoassimilate partitioning, carbohydrate content in the storage taproot, and respiration of selected plant parts in Canada thistle.

MATERIALS AND METHODS

Separate $^{14}CO_2$ pulse-chase experiments were conducted in the field, greenhouse, and growth chamber.

Field experiment. Canada thistle plants were carefully dug from soil during the 1987 growing season to provide a root system with a corresponding ball of soil the equivalent of a 20-L pot. A minimum of 10 plants were dug during the first week of each month of the growing season, placed in pots, watered, and then allowed to equilibrate outside for 5 d. Five vigorous and uniform plants were selected as experimental material. A single leaf midway down the stem was enclosed in an airtight 2-L plastic bag.

A corner of each bag was injected with 55 nmole $[^{14}C]NaHCO_3$ (11.1×10^7 Bq mmol^{-1}) dissolved in 25 µl H_2O and followed immediately with 100 µl 0.5 N HCl to release $^{14}CO_2$. After 30 min under field conditions, 3 ml 0.5 N KOH was added to absorb residual CO_2. Plants were harvested 48 h after the $^{14}CO_2$ pulse and individual parts frozen immediately in liquid N, lyophilized, and ground to pass a 10-mesh screen, and an aliquot was analyzed[4] for ^{14}C (24). Experimental design was completely randomized with five replications (one plant per replication).

Greenhouse experiment. Canada thistle seed was germinated in 1987 on February 11 and 24 plus March 3 and 17 to provide plants growing at four stages of development: rosette-like (hereafter called rosette), rapid stem elongation (hereafter called bolt), floral bud, and full flower. These plants were grown in a greenhouse (28 ± 3 C, 14-h photoperiod under full-spectrum metal-halide lamps, 750 µE m^{-2} s^{-1} photosynthetically active radiation), and watered as needed. The pulse-chase and harvesting procedures outlined above were used in this experiment beginning on April 28, 1987 except that all plants were kept in a greenhouse. Experimental design was completely randomized with five replications (one plant per replication).

Growth chamber experiment. A growth chamber experiment was designed to examine the effects of two selected environmental regimes on respiration of selected plant parts, ^{14}C-assimilate distribution and size of carbohydrate storage pools.

Plants. Plants were started from seed June 20, July 28, and August 16, 1988 and grown (14-h photoperiod, 30/26 C day/night, 160 µE m^{-2} s^{-1} photosynthetically active radiation) to provide plants concurrently in the rosette, bolt, and flower bud stages of development. For 2 wk before treatment, half the plants from each growth stage were placed in a simulated early-fall environment (12/18 C night/day, 12-h photoperiod) or in a simulated late-spring environment (21/28 C night/day, 15-h photoperiod). Fifteen hours before treatment, all plants were placed in a spring environment and uniform rates of photosynthesis were confirmed[5]. Plants were pulsed as described for the field experiment except that 92 nmole $[^{14}C]Na_2CO_3$ (202×10^7 Bq mmol^{-1}) was used and plants treated with ^{14}C for only 20 min. Pulsed leaves had the same leaf area and were at the sixth, seventeenth, and twenty-eighth internodes above the root collar of the rosette, bolt, and bud stages, respectively. Plants were returned immediately to the fall or spring environments after pulse. Leaf disks were sampled at selected intervals for 24 h after the pulse in a pattern from the leaf apex toward the base. Disks were placed in 80% ethanol and extracted ^{14}C was quantified by liquid scintillation spectroscopy.

Respiration. Plants were harvested the day after pulse treatment, and respiration of shoot and root apices plus taproot segments (approximately 200 mg per segment) was measured[6]. Plant parts were individually placed in 7-ml flasks containing 2 ml 30-mM buffer (3-morpholino-2-hydroxy-propansulfonsoure), pH 6.5, with 1mM $CaCl_2$; 0.2 ml 1.8 M KOH was placed in the center well to absorb CO_2. Tissue was equilibrated 10 min and manometric measurements were taken every 10 min thereafter for 30 min. Respiration was measured at 15 and 25 C (for fall and spring plants, respectively) and values were adjusted to standard temperature and pressure.

Physical fate. All plant parts, including those used to measure respiration, were frozen, lyophilized, ground, and analyzed for ^{14}C content as described for the field experiment.

Metabolic fate. Low molecular weight sugars (mostly glucose, sucrose, fructose, and short-chain fructans) were extracted with near boiling 95% by vol ethanol, and high molecular weight sugars (longer chain fructans or inulin) were subsequently extracted from the same samples with near boiling water (19). Starch was not assayed since no starch was found with KI stain assay (7) or by glucose assay following amyglucosidase (EC 3.2.1.3) digestion[7].

Low molecular weight sugars were estimated by evaporating alcohol from the initial extraction, dissolving the residue in water, passing the extract through a column[8], and injecting into a high-pressure liquid chromatograph equipped with a refractive index detector (aqueous mobile phase of 0.01-mM disodium-calcium salt ethylenediamine tetraacetic acid, at 0.5 ml min^{-1}; column[9] at 80 C). The high molecular weight fraction was converted to simple sugars by acidifying to pH 2.0 with 0.4 N HCl and boiling for 2 min followed by neutralization with 0.4 N NaOH, column passage, and injection on the high-pressure liquid chromatograph. Frac-

[4]Packard Biological Oxidizer. Packard Instrument Co., 1 State St., Meriden, CT 06450.

[5]Li-Cor, Inc., 4421 Superior St., P.O. Box 4425, Lincoln, NE 68504.

[6]Gilson Differential Respirometer. Gilson Medical Electronics, 3000 W. Beltway Hwy., Middleton, WI 53562.

[7]Sigma Chem. Co., P.O. Box 14508, St. Louis, MO 63178.

[8]Amberlite MB3. Biorad, P.O. Box 708, 220 Maple Ave., Rockville, Centre, NY 11571.

[9]Sugar Pak. Waters Chromatography Div., 34 Maple St., Milford, MA 01757.

Table 1. Distribution of ^{14}C assimilate 48 h after $^{14}CO_2$ pulse of field-grown Canada thistle at different times during the 1987 growing season[a].

Date pulsed	Plant growth stage	Total ^{14}C assimilated	^{14}C distribution			Dry weight	
			Shoot	Donor	Root	Shoot	Root
						g	
5/7	Bolt		37 ab		42 a	1.5 c	2.2 ab
6/5	Bud		52 a		9 c	7.2 b	2.5 ab
7/1	Flower		39 ab		23 b	12.8 a	3.6 a
8/7	Post-flower		35 ab		10 c	13.4 a	3.2 a
9/4	Post-flower		55 a		11 c	19.0 a	3.2 a
10/9	Bolt		15 b		54 a	0.5 c	1.0 bc
11/4	Bolt		18 b		21 b	0.9 c	0.7 c

[a]Means within columns followed by the same letter are not significantly different at the 5% level using Fisher's Protected LSD Test.

tions (0.5 ml) were collected and radioactivity assayed by liquid scintillation spectroscopy. Tissue residues were oxidized, and released $^{14}CO_2$ was assayed (24). Carbohydrate quantities were verified by separation on thin-layer silica gel plates[10], staining with urea (28), and locating ^{14}C with an image scanner[11]. Stained and ^{14}C zones were scraped and hydrolyzed (0.6 N HCl), and an aliquot was measured for ^{14}C by liquid scintillation spectrometry. Individual sugars were measured after hydrolysis colorimetrically for glucans with glucose oxidase or for fructans with resorcinol (3).

Experimental design. A factorial design was used with growth stage and environment as the main effects. Five replications were used, one of which was evaluated for assimilate distribution by autoradiography (6). The experiment was repeated with plants in the rosette and bolt, but not the flower stage. Both experiments reflected the same trends and results are presented for the first experiment. Individual means were separated by Fisher's Protected LSD Test at the 5% level and main effects of environment and growth stage were separated by orthogonal contrasts.

RESULTS AND DISCUSSION

Field experiment. Total ^{14}C fixed was low early and late in the season (Table 1). Roots of bolting plants pulsed on May 7 and October 9 contained a higher percentage of fixed ^{14}C-assimilate than shoots or donor leaves. However, the concentration (dpm g^{-1} dry weight) of ^{14}C-assimilate in roots was less in May and October than in June and July due to low assimilation early and late in the season (data not shown). Roots contained a greater quantity of ^{14}C-assimilate in June, July, and August than in May, September, October, and November although the percentage of fixed ^{14}C-assimilate in the root was less from June through September than in May and October. The least assimilate export from the donor leaf occurred on November 4. Leaves were still green and appeared robust on this date. Root ^{14}C content was not correlated with root biomass or root-to-shoot ratio (data not shown) suggesting that a factor other than sink size controlled assimilate accumulation.

[10]Silica gel 250F. J. T. Baker Chem. Co., Phillipsburg, NJ 08865.
[11]Bioscan, Inc., 4590 MacArthur Blvd., N.W., Washington, DC 20007.

Greenhouse experiment. More assimilate was retained in donor leaves of the flower bud (63%) than the bolt stage (26%) of development (Figure 1). Export of ^{14}C-assimilate to the shoot apices was greatest during the rosette and bolt stages, but declined by nearly half when flower buds became evident. Assimilate levels were greater in the lateral and taproots of plants in the rosette and bolt than the flower bud stage. This generally agrees with results from the field experiment.

Growth chamber experiment. There was no environment × growth stage interaction for any of the parameters measured in the growth chamber experiment. Growing conditions (fall versus spring) prior to pulse treatment did not affect photosynthesis within a particular stage of development (Table 2). Photosynthesis in the donor leaf was greatest in the rosette, less in the bolt, and least in the flower bud stages (Table 2). The same residual ^{14}C remained in donor leaves of all development stages and both environments (Table 3). These data suggest that photosynthetic rates are greater in young growth stages resulting in greater assimilation and translocation of the carbon during the 24 h following assimilation. However, plants at the bolt stage will probably export a greater quantity of assimilate on a whole plant basis than rosette plants due to a larger total leaf area (Tables 2, 3).

More ^{14}C accumulated in lateral roots of plants grown under fall than spring conditions (Table 3). Approximately 22 and 7% of the total fixed ^{14}C moved to roots in a fall and spring environment, respectively. Canada thistle was shown to accumulate carbohydrate reserves in the fall (9, 26). This is attributable to shoot tip respiration being less in fall compared to spring conditions whereas lateral root and taproot respiration remained constant in the two environments (Table 2). Change in sink competition between root and shoot may be one explanation for more assimilate movement to the root in fall conditions. Kallarackal and Milburn (12) reported that reduced root respiration in chickpea (*Cicer arietinum* L.) made the root less competitive with developing fruit as a sink for translocated sucrose. Khayat and Zieslin (14) reported that sink activity of upper shoots in roses (*Rosa* sp. hybrids) declined as nighttime temperatures decreased from 18 to 12 C

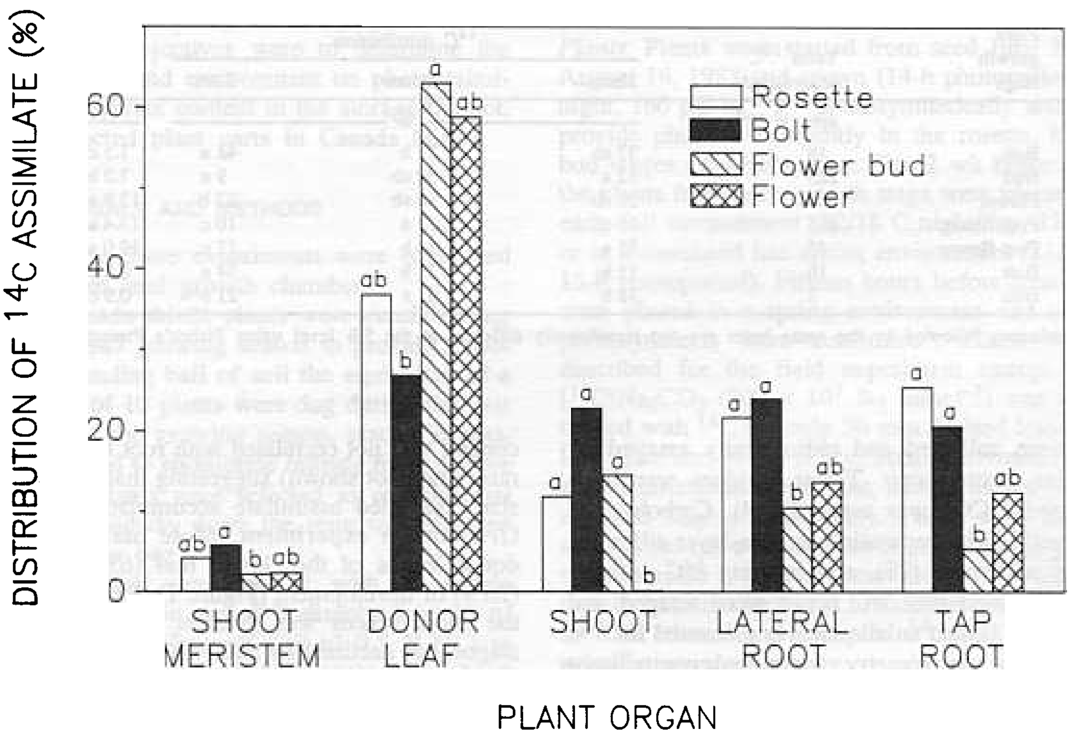

Figure 1. Assimilate distribution within Canada thistle growing in a greenhouse at different stages of development. Means within plant organ with the same letter are not significantly different at the 5% level using Fisher's Protected LSD Test.

resulting in decreased assimilate import. More assimilate moved to roots under 12 than 18 C conditions. It was shown that relative translocation of assimilates to roots of 7-wk-old Canada thistle was greatest under conditions simulating the fall season, although total movement of assimilate may have been greater at other times of the year (18), perhaps due to a morphological or phenological effect on the quantity of carbon fixed.

If root reserves are critical for survival, then weed management strategies might be served best by altering assimilate partitioning. Some foliar systemic herbicides are recommended for application at the flower bud stage or later (8). An alternative approach to controlling Canada thistle could include timing herbicide applications to capitalize on the natural pattern of assimilate movement in the phloem to the root. Consequently, herbicides might perfuse the root system more thoroughly in fall or early spring before temperatures increase and provide more effective control.

Several investigators have found more extensive distribution of herbicides and better control of weeds by applying

Table 2. Morphological and physiological parameters of Canada thistle plants grown in a simulated fall or a spring environment and at different growth stages[a].

		Leaf area		Photosynthesis		Respiration			Dry weight	
Environment	Plant growth stage	Donor leaf	Whole plant	Donor leaf	Whole plant	Shoot tip	Tap-root	Lateral root	Shoot	Root
		cm^2		$mg\ CO_2\ m^{-2}\ s^{-1}$	$mg\ CO_2\ s^{-1}$	$\mu l\ O^2$ consumed $gm\ fw^{-1}\ min^{-1b}$			g	
Fall	—	39 x		0.48 x	0.03 x	4.5 y	1.6 x	1.7 x	3.5 x	9.2 x
Spring	—	40 x		0.58 x	0.04 x	8.4 x	1.7 x	2.3 x	3.0 y	7.4 x
—	Rosette	35 a		0.78 a	0.02 b	6.9 ab	1.9 a	2.4 a	2.7 b	1.1 c
—	Bolt	45 b		0.52 b	0.06 a	8.1 a	1.7 a	2.2 a	2.9 b	8.6 b
—	Bud	39 ab		0.28 c	0.03 b	4.4 b	1.4 a	1.3 b	4.2 a	15.1 a

[a]Environment averaged over growth stage. Growth stage averaged over environment. Means within columns for environment or growth stage followed by the same letter do not differ at the 5% level.

[b]Standard temperature and pressure.

Table 3. Distribution of ^{14}C assimilate 24 h following $^{14}CO_2$ pulse of Canada thistle plantas grown in a simulated fall or spring environment and at different growth stages[a].

Environ-ment	Plant growth stage	Total ^{14}C assimilated	^{14}C distribution								
			Shoot			Root				Total exported from donor	
			Top	Apex	Donor	Base	Lateral	Tap	Second	Shoot	Root
			% of ^{14}C assimilated								
Fall	—		1 y	8 x	48 x	9 x	22 x	11 x	1 x	18 y	34 x
Spring	—		3 x	12 x	55 x	13 x	7 y	8 x	2 x	28 x	17 y
—	Rosette		3 a	12 a	54 a	3 b	16 a	11 a	1 b	19 a	27 a
—	Bolt		2 a	9 a	53 a	14 a	13 a	9 a	1 b	24 a	23 a
—	Bud		2 a	9 a	48 a	15 a	14 a	8 a	4 a	26 a	25 a

[a]Environment averaged over growth stage. Growth stage averaged over environment. Means within columns for environment or growth stage followed by the same letter do not differ at the 5% level.

herbicides at younger than older growth stages (5, 13, 25). The growth stage which is more suitable for herbicide translocation in Canada thistle is equivocal. Rosette plants had the highest photosynthetic rate per unit leaf area whereas bolted plants fixed the most carbon per plant (derived by multiplying treated leaf photosynthesis by whole plant leaf area) (Table 2). Assuming uniform foliar coverage and herbicide export from leaves, bolted plants would export more herbicide to roots because of the larger whole plant leaf area. However, the concomitant increase in root system size in later growth stages (Table 2) would likely "dilute" a herbicide that is translocated equally to all parts of a root. Regression analysis demonstrated no relationship between root ^{14}C-assimilate content and root biomass (data not shown). Therefore, there is no evidence that basipetal transport of assimilate will be enhanced by larger roots. Results from the current experiment suggest that younger growth stages are appropriate for basipetal transport of assimilates, and possibly herbicides, when photosynthesis rates are high.

Environment conditions did not influence root concentrations of sucrose, glucose, fructose, fructan polymers, or ^{14}C-assimilate distribution to each of those components. In contrast, roots of rosette plants had greater concentrations of glucose and fructose (low molecular weight fraction) than did bolt plants, which in turn had greater concentrations than roots of the bud stage (Table 4). Rosette plant roots also had higher ^{14}C residues than bolt or bud plant roots. It is likely that the residue fraction corresponds to structural forms of carbon that would not have been extracted by alcohol or water (27). There were greater concentrations of fructan polymers (high molecular weight fraction) in the bolt and bud stage roots than rosette roots. These were apparently longer chains in the bolt and bud stage roots than in rosette roots based on the high fructose-to-total sugar ratio of the hydrolyzed, high molecular weight component. Fructans are polymers of fructose with sucrose as an end group (19). More ^{14}C was integrated into long-chain polymers (high molecular weight component) of the bolt and bud growth stages, indicating a physiological shift in usage of current photoassimilate. In the rosette stage, more photoassimilate may have been utilized for growth, whereas at the bolt and bud stages increasing amounts of photoassimilate may accumulate as

Table 4. Carbohydrate content and ^{14}C-assimilate distribution among carbohydrate fractions of the taproot of Canada thistle grown in a simulated fall or spring environment and at different growth stages[a].

Environ-ment	Plant growth stage	Carbohydrate content									^{14}C distribution		
		Low molecular weight				High molecular weight							
		Suc[b]	Glu	Fru	Total	Suc	Glu	Fru	Total	Fru ratio	Low M.W.	High M.W.	Residue
		% dry weight									% of total ^{14}C		
Fall	—	0.56 x	0.53 x	0.36 x	1.5 x	3.1 x	3.6 x	18.4 x	25.1 x	0.68 x	13 x	61 x	26 x
Spring	—	0.59 x	0.44 x	0.35 x	1.4 x	3.0 x	3.7 x	14.1 x	22.1 x	0.66 x	11 x	64 x	25 x
—	Rosette	0.60 a	0.66 a	0.45 a	1.7 a	3.1 a	4.1 a	11.9 b	18.7 b	0.58 b	9 b	46 b	45 a
—	Bolt	0.59 a	0.39 b	0.31 b	1.3 b	3.2 a	3.4 ab	19.5 a	27.7 a	0.72 a	11 ab	67 a	22 b
—	Bud	0.42 a	0.17 c	0.16 c	0.7 c	2.6 a	2.5 b	23.5 a	28.5 a	0.81 a	16 a	73 a	11 b

[a]Environment averaged over growth stage. Growth stage averaged over environment. Means within columns for environment or growth stage followed by the same letter do not differ at the 5% level.

[b]Suc = sucrose, Glu = glucose, Fru = fructose, M.W. = molecular weight, Fru ratio = fructose concentration/total carbohydrate concentration of the hydrolyzed water fraction.

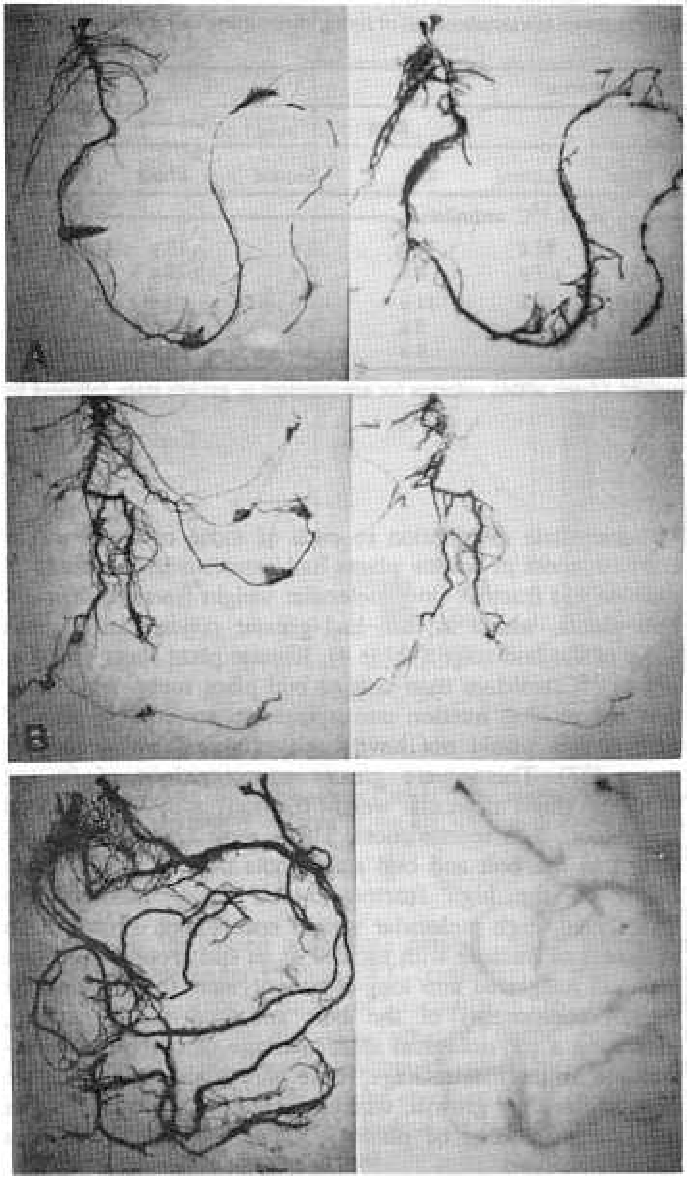

Figure 2. ^{14}C-assimilate distribution in roots of Canada thistle grown under simulated spring conditions at the (A) rosette, (B) bolt, or (C) bud growth stage. Plants are on left and autoradiographs are on right.

reserves. Metabolic steps controlling fructan polymer length were implicated in control of phloem unloading and, consequently, phloem transport (21). In Canada thistle, direction and extent of movement in the phloem appears to be controlled by different processes: growth at early stages and storage at late stages of growth.

Autoradiographs revealed ^{14}C-assimilate to perfuse roots more thoroughly than shoots. The ^{14}C label was notably present in shoot apices and was at a much lower concentration throughout the stem (data not shown). In contrast, autoradiographs demonstrated fairly uniform distribution of ^{14}C-assimilates throughout the root system (Figure 2). Autoradiographs of root cross sections showed the cortex absorbed significant ^{14}C (data not shown).

In the growth chamber experiment, environment affected carbohydrate partitioning between root and shoot more strongly than did growth stage. Photosynthetic rates for the growth stages were similar regardless of the previous 2-wk environment. Reduced temperatures in the fall conditions reduced sink strength of shoot apices by decreasing shoot tip respiration, and assimilate moved preferentially to lateral roots. In older Canada thistle plants, there was a shift from carbohydrates utilized in growth to carbohydrates stored as reserves. From a practical viewpoint, the results of this research suggest that maximum basipetal translocation of herbicides in Canada thistle may occur in early spring or fall. Methods of simulating environmental inhibitory effects on shoot apices, such as growth regulator applications, might provide new opportunities to manage Canada thistle.

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